

RETICULATE EVOLUTION IN *COLYMBETES*  
(COLEOPTERA: DYTISCIDAE)

JAMES R. ZIMMERMAN

Dept. of Biology, New Mexico State University, Las Cruces 88003

---

An unusual situation was discovered in a recent revision of the *Colymbetes* of North America (Zimmerman, in press). Species problems in the genus proved to be particularly vexing and unusual, and the relationship between 2 western species is most intriguing and seems worthy of reporting separately. This issue of this journal which is dedicated to Hugh Leech who provided much of the material for the study of these two species is a particularly appropriate time and place to present this interesting relationship.

*Colymbetes* species are some of the larger and more derived members of the subfamily Colymbetinae (Sharp 1882, Balfour-Browne 1950). The North American species are easy to recognize because of their size (up to 20 mm) and the transverse grooves on the elytra (Figures 10, 13). There are 7 species in North America and about 13 in Eurasia. Three are found in both hemispheres. It is a holarctic group with no representatives south of North Africa and the Arabian Peninsula.

The North American species can be separated into 3 groups. Three species, *dolobratus* Paykull, *exaratus* Leconte (not of authors), and *sculptilis* Harris readily fall into one group and *dahuricus* Aubé and *paykulli* Erichson fall into another. The 2 species of this report, *densus* Leconte (= *exaratus* of authors) and *strigatus* Leconte occupy an intermediate position to those two groups. The separation is based mainly on the structure of the male pro- and mesotarsi, but there are other characters which support the groupings.

#### Geographical Distribution

*C. strigatus* and *densus* are found from southern California to southern Alaska. Each is composed of 2 geographical races (Fig. 1). *C. s. strigatus* extends from the vicinity of San Diego to near San Francisco. It appears to be mainly confined to inland localities with the exception of old records from near San Diego and Los Angeles. It occurs in both mountainous regions and comparatively low-lying areas in the Central Valley. Nowhere is it common.

*C. s. crotchi* Sharp, the northern race of *strigatus*, is found from Monterey County to Humboldt County in a narrow band hardly more than 50

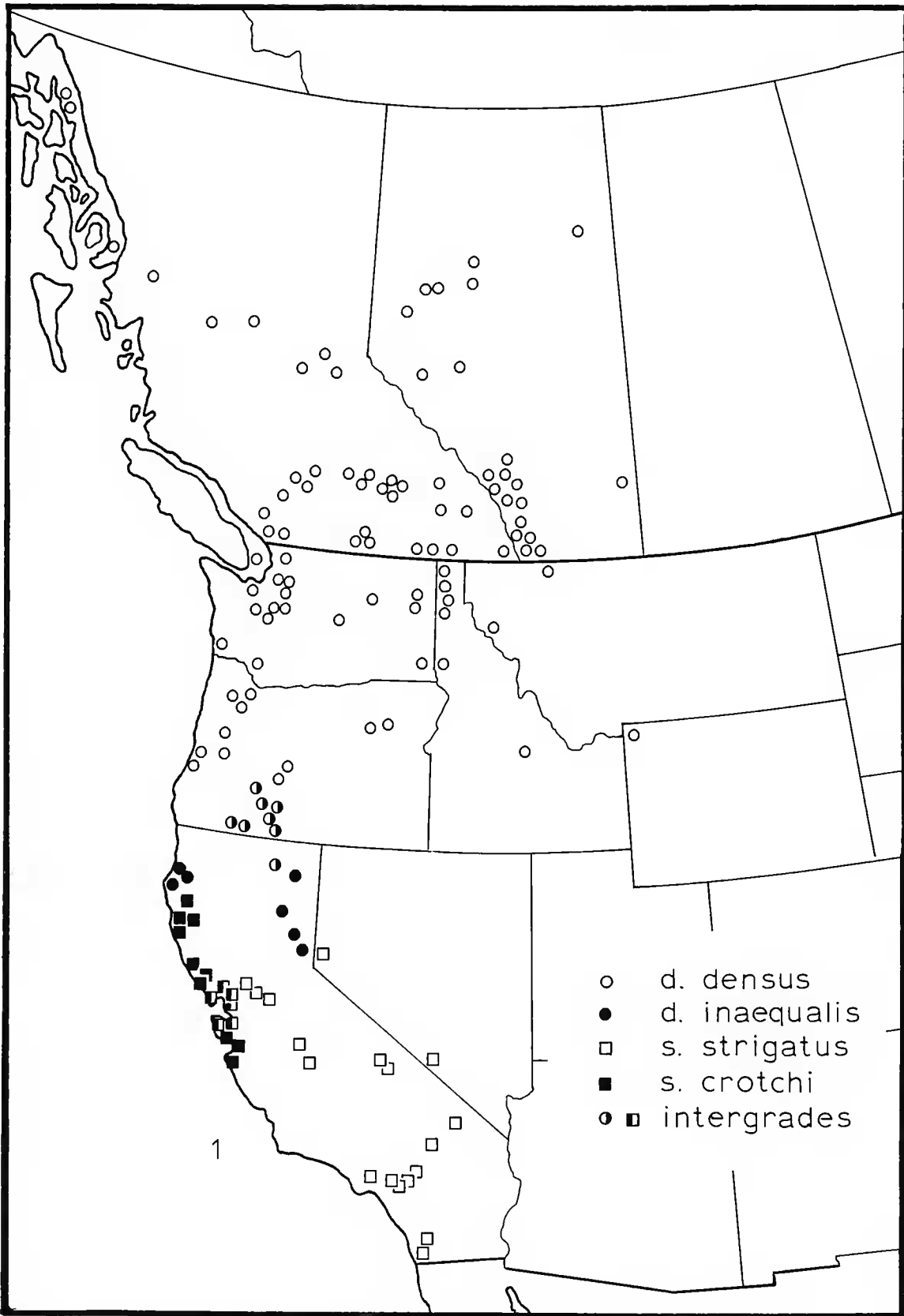


Fig. 1. Distribution of *Colymbetes densus* and *C. strigatus*.

miles inland. It can be found in estuarine habitats along the coast and in pools in the low coast ranges nearby.

Intergrades between the two races of *strigatus* are common in the area surrounding San Francisco Bay. They are easy to detect because of the marked differences (for the genus, that is) between the races. Actually, the

Table 1. Comparison (mm) of 8 mensural characters in *Colymbetes strigatus* and *densus*.

Character	(N)	Subspecies				
		<i>s.</i> <i>strigatus</i> (southern)	<i>s.</i> <i>strigatus</i> (northern)	<i>s. crotchi</i>	<i>d.</i> <i>inaequalis</i>	<i>d. densus</i>
length	24	15.95 ± 0.80	16.55 ± 0.57	17.99 ± 0.65	17.08 ± 0.53	16.93 ± 0.59
width	24	7.64 ± 0.31	7.97 ± 0.30	8.58 ± 0.27	8.08 ± 0.20	8.05 ± 0.27
femur length	24	3.75 ± 0.25	3.82 ± 0.13	4.19 ± 0.10	4.09 ± 0.10	4.05 ± 0.12
femur width	24	1.16 ± 0.07	1.19 ± 0.05	1.30 ± 0.06	1.28 ± 0.05	1.26 ± 0.06
tibial length	24	3.29 ± 0.25	3.35 ± 0.13	3.72 ± 0.09	3.60 ± 0.09	3.57 ± 0.12
tarsal length	24	2.64 ± 0.28	2.69 ± 0.13	3.21 ± 0.11	3.20 ± 0.11	3.14 ± 0.15
aedeagus	10	4.48 ± 0.26	4.93 ± 0.24	6.61 ± 0.20	5.97 ± 0.20	5.70 ± 0.19
width of protarsomere	10	0.68		0.83	0.87	0.88

influences of *crotchi* on *strigatus* can be found on numerous specimens which occur some distance from the zone of intergradation. This influence shows not only in the male tarsi, but also in mensural characters (Table 1).

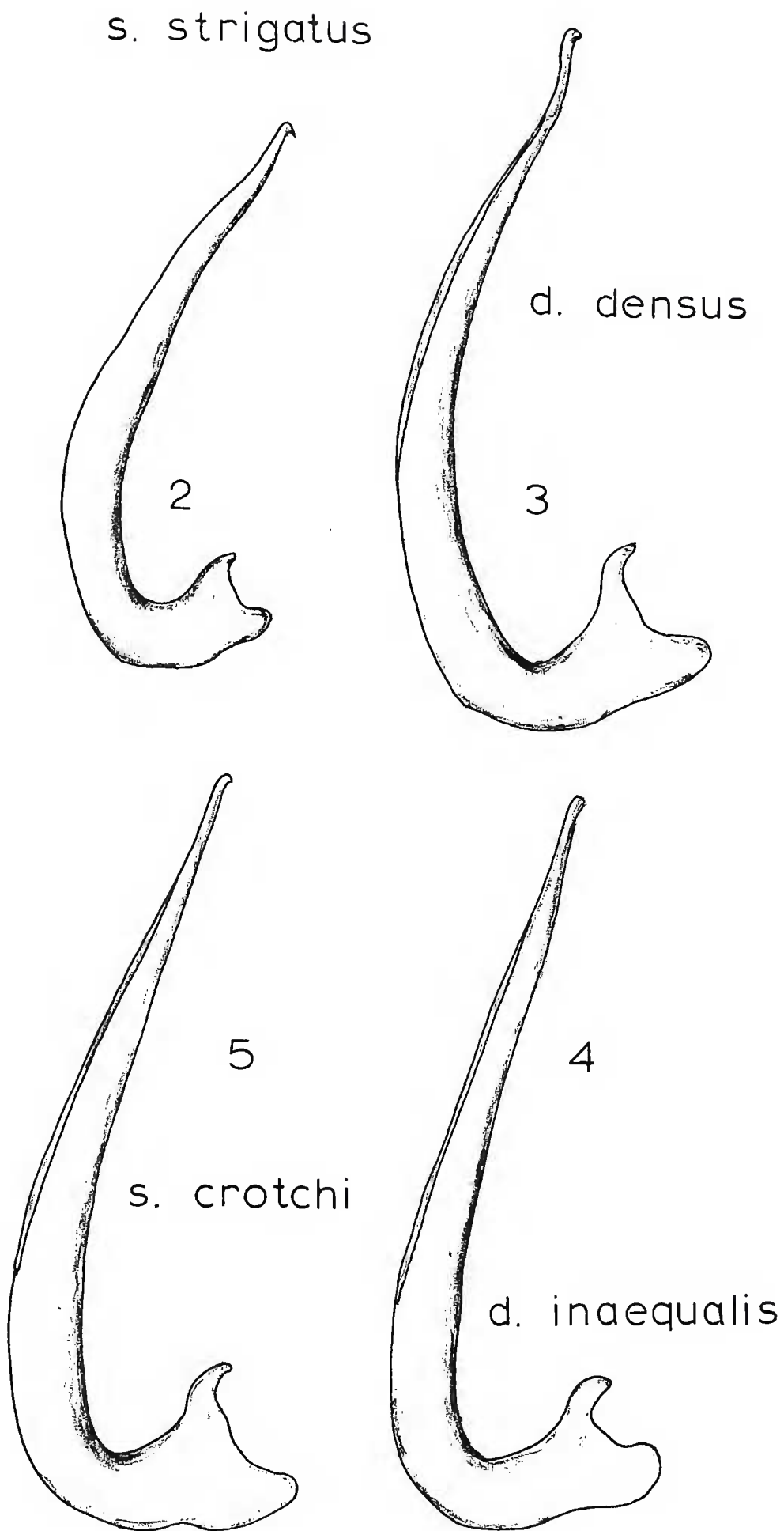
*C. d. densus* is the most widely distributed of the 4 races of these 2 species. Its range is from southern Alaska to Oregon and inland to Alberta and Wyoming. It intergrades with *d. inaequalis* Horn in southeastern Oregon and Siskiyou County, California.

The known distribution of *d. inaequalis* is limited to 2 separated areas—one in the northern Sierra Nevadas including Mt. Lassen, and the other in Humboldt County on the coastal lowlands and at a few sites slightly more inland. Specimens from the two areas are quite similar and do not appear to merit subspecific separation. The gap between them may be due more to lack of collecting than any real discontinuity in distribution. It is evident, however, that two contrasting habitats are used by the two populations.

As far as is known, the two species, *strigatus* and *densus*, are allopatric to one another. The Sierra populations of *d. inaequalis* and *s. strigatus* approach each other and may occur together, but these rather rare taxa have not yet been taken together. Also, *d. inaequalis* and *s. crotchi* are both found in Humboldt County, but there is still a separating gap of 50 to 75 miles.

#### Species Limits and Anatomical Relationships

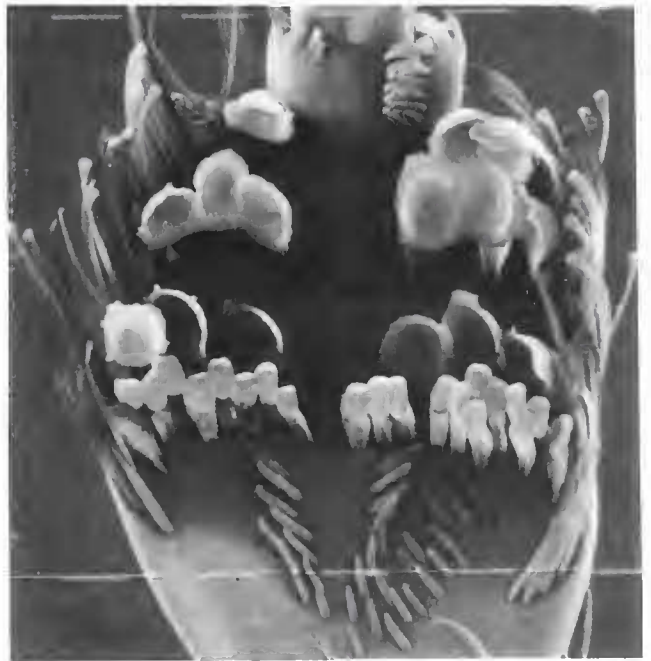
The unusual feature of these 2 species is that *strigatus crotchi* bears a closer anatomical relationship in most characters to *densus inaequalis* than to *s. strigatus*. If it were not for the unmistakable series of intergrades between *s. crotchi* and *s. strigatus*, one would surely conclude that *s. crotchi* was an allopatric conspecific relative of *d. inaequalis*.



Figs. 2-5. Lateral views of aedeagi of subspecies of *Colymbetes densus* and *C. strigatus*.



6



7



8

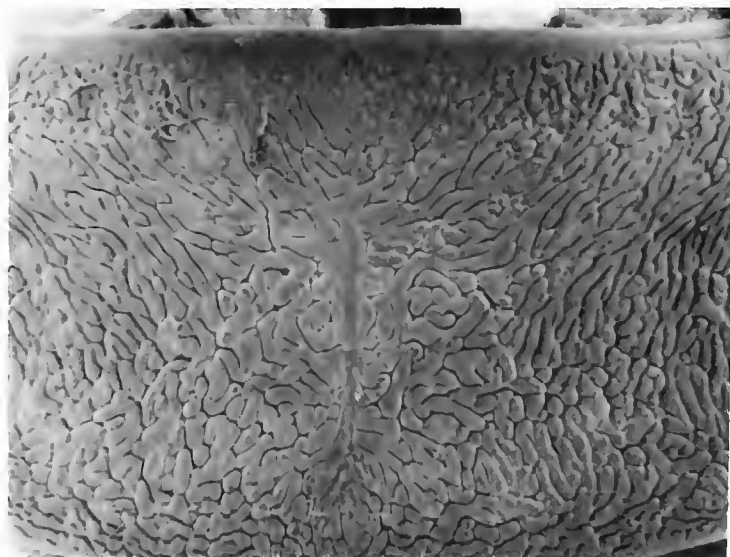
9



Figs. 6-9. Protarsi of 6) *C. s. strigatus* from Fresno Co., 7) *C. s. strigatus* from Yolo Co., 8) *C. s. strigatus* from San Diego Co., and 9) *C. s. crotchi* from Marin Co.



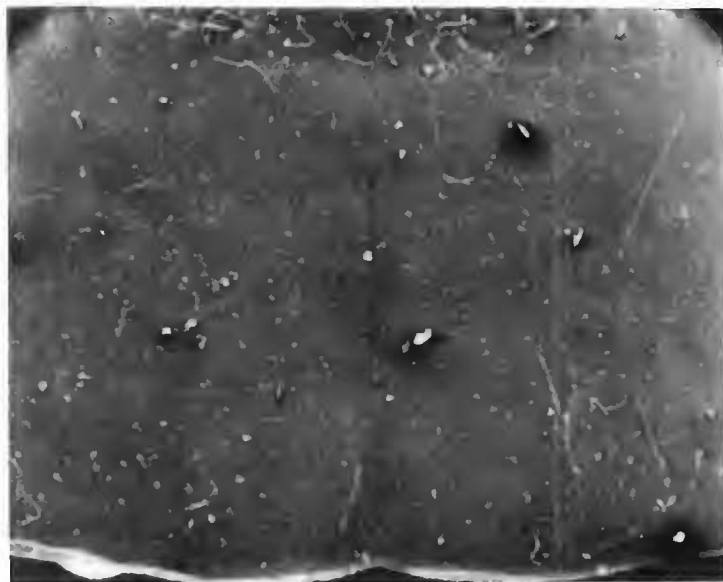
10



11

13

12



Figs. 10–13. Fig. 10. SEM of discal area of the elytra of female of *C. d. inaequalis* from Humboldt Co. Fig. 11. SEM of female pronotum of *C. d. inaequalis* from Humboldt Co. Fig. 12. SEM of pronotum of female of *C. s. crotchi* from Marin Co. Fig. 13. SEM of discal area of the elytra of male of *C. sculptilis*.

The relationship is apparent through their size, shape, sexual characters, and in habitat utilization. Table 1 is a comparison of 8 mensural characters including the length of the aedeagus. In all of those characters *s. crotchi* is closer to *d. inaequalis* than to the two samples of *s. strigatus*. Configuration as well as overall length of the aedeagus is more similar also (Figs. 2–5).

The most striking character is the nature of the male pro- and mesotarsi. There are 2 distinct types of tarsal adornment in *Colymbetes* as indicated

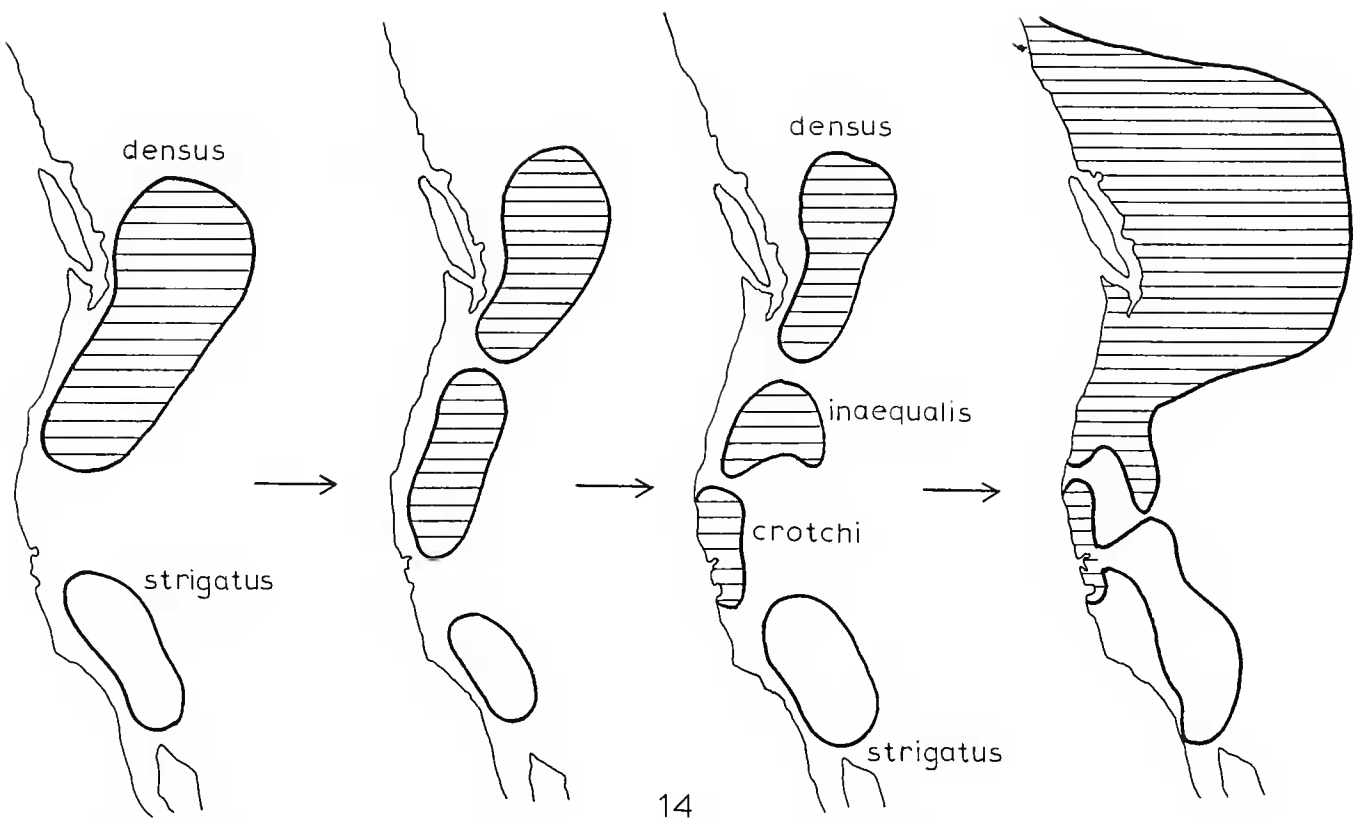


Fig. 14. Diagram of reconstruction of probable isolation and subsequent joining of populations leading to present situation in *C. densus* and *C. strigatus*.

in the introduction. The most common and probably the ancestral type is the condition with enlarged flattened "palettes"—rounded adhesive discs as seen in Figure 8. This is the type found in the southernmost populations of *s. strigatus*. Populations to the north show a transition in the basal row of palettes. The size of the terminal disc decreases and tends to become a double row of 25 or more (Figs. 6, 7). This condition is what Leech recognized in his key to the California species (Leech and Chandler 1956).

The other type of adhesive structures and probably the derived condition, is that found in the *dahuricus* group. The adhesive structures take the form of over a hundred or more stout setae with slightly expanded tips.

There is an intermediate condition, however, and it is found in both races of *densus* and in *strigatus crotchi*. The basal group of adhesive structures in these are setae, but the distal ones are palettes (Fig. 9). The cline in size and number of palettes in *s. strigatus* appears then to be introgression of the genes for the setal form from *s. crotchi*.

Other characters which intergrade in *strigatus* are the shape and length of the aedeagus, overall size, the amount of secondary mesh on the pronotum, and the degree of swelling of the frons next to eye above the antennal base.

Intergradation in *densus* is seen primarily in two characteristics, both sexual. The two races are so similar in other characters that it is quite difficult to find differences. The aedeagus of *d. densus* is distinctive in that it is strongly curved laterally before the apex while that of *d. inaequalis* is

only slightly so (Fig. 3, 4). Intermediates to these conditions can readily be recognized with experience. The females of *d. inaequalis* have the elytra duller (velvety) than any other North American *Colymbetes*. This is due to the widening of the elytral grooves and the strong development of the surface microreticulation on the interspaces between the grooves (Fig. 13). In its most extreme form this condition covers the anterior  $\frac{4}{5}$  or more of the elytron. The intergrades have variable amounts of the elytron so affected. The condition is found to some degree in a few females from throughout the range of *d. densus*.

Characters which indicate a close affinity between *d. inaequalis* and *s. crotchi* are seen in the male tarsi, frons swollen above the antennal base, the pale subsutural line, in the similarity of the size and shape of the aedeagus, and the general size and shape of the whole animal. In fact, there are only 2 characters which permit ready separation, but fortunately these are ones that are easily evaluated. The smooth pronotum of *s. crotchi* in contrast to the pebbled surface on that of *d. inaequalis* (Figs. 11, 12) is a character that can be discerned even in the field with but a hand lens and serves as an excellent indicator of the presence of mixing or not. The smooth pronotum is a character unique to *s. crotchi* and can be used to separate it from any other North American *Colymbetes*.

The second feature is the previously mentioned velvety appearance of the female elytra in *d. inaequalis*, but which is not present in *s. crotchi*. It, of course, is useful only in comparing females, but in many species of dytiscids only the male serves in verification of intergradation.

### Evolutionary Considerations

The evidence is clear that *C. strigatus* is composed of two rather different races. The southern race, *strigatus*, would readily be placed in the *sculptilis* group of species, i.e., the group with only palettes on the male tarsi; but *s. crotchi* is so similar to *densus*, which has setae (which seem to be a derived character) as well as palettes, that one would include it with that species if there were not intergradation between these two.

One has to conclude that *crotchi* originally was derived from ancestral *densus*, separated from that species, and has subsequently come into contact with *strigatus* and in the absence of any reproductive barrier merged with it. The geographical positions of the 4 taxa support this view. The possible sequence of events is diagrammed in Figure 14.

Originally *strigatus* and *densus* were separate species. At this time we lack enough evidence to show their probable origins, and it is even possible that *densus* arose from ancestral *strigatus*. The reverse seems improbable because of the greater number of derived characters in *densus*.

*C. densus* divided into 2 populations and later the southern one of those divided again. The first division led to a group which could use not only



mountainous areas, but also low-lying coastal ponds including the brackish water in quiet estuaries along the California coast. The second division resulted in what are now recognized as *d. inaequalis* in the north and *s. crotchi* in the south. *C. d. inaequalis* occupies both inland and coastal areas as we see today, but *s. crotchi* encountered *strigatus* inland and in the absence of reproductive barriers interbred with it.

As interpreted here, ancestral *strigatus* is apparently derived from the *sculptilis* group. The origin of the ancestral *densus* is problematical. Apparently it has no sister-species in the Old World, because no species has been reported from there which have both setae and palettes on the male tarsi. The presence of setae, larger size, and darker pigmentation are characters which link *densus* and *s. crotchi* to *dahuricus* and *paykulli* and not to the more pleisomorphic *sculptilis* group.

It is possible that ancestral *densus*, which contained what is now *inaequalis* and *crotchi* is a vicariant of ancestral *strigatus*. If so, it had undergone considerable differentiation as evidenced by the male tarsi, expansion of the frons, larger size, and aedeagi. The fact that *s. crotchi* does not show any evidence of intergradation with *d. inaequalis* supports the view that the former had become specifically distinct from the latter. It is true that there exists a slight gap between the ranges of the two, but even so some of the specimens I have examined should show admixture. The gap is due to lack of collecting and does not reflect the real distribution in my opinion. It would be much better if sympatry or intergradation could be shown, however.

It still appears *s. crotchi* had differentiated into a separate entity and has now reunited with *s. strigatus* with the introgression of characters into the latter and separation from *d. inaequalis*. A pattern of hybridization and reticulate evolution is thus realized.

If intermediates are found between *crotchi* and *inaequalis*, then all four geographical entities will be included in *strigatus*. With the evidence at hand, I am hesitant to make a nomenclature change. Those who feel that one species disappears when a speciation event occurs will differ with my interpretation of this situation, but as yet I can not accept that view of species and their evolution.

### Literature Cited

- Balfour-Browne, F. 1950. British Water Beetles. Vol. 2, Ray Society, London.
- Leech, H. B., and H. P. Chandler. 1956. Aquatic Coleoptera, *In* Usinger's Aquatic Insects of California. Univ. California Press, Berkeley and Los Angeles.
- Sharp, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae. Sci. Trans. Roy Dublin Co., 2:179-1003.
- Zimmerman, J. R. 1980. The use of multivariant analysis in the study of species problems in the *sculptilis* group of *Colymbetes* (Coleoptera: Dytiscidae). Coleop. Bull., 34: 213-226.
- Zimmerman, J. R. *In press*. A revision of the *Colymbetes* of North America. Coleop. Bull.